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CHROMOSOME NUMBERS AND EVOLUTION IN *ANODA* AND *PERIPTERA* (MALVACEAE)

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ABSTRACT

Relationships within and between the principally North American, malvaceous genera *Anoda* and *Periptera* are assessed through analysis of chromosomal and hybridization data. Chromosome numbers are reported for ten species of *Anoda* and one of *Periptera,* and observations on meiosis in hybrid and nonhybrid plants are presented. The results indicate: 1) that *Anoda* and *Periptera* are closely related and occupy a relatively isolated position in the tribe Malveae, 2) that speciation in *Anoda* has occurred primarily at the diploid level, $n = 15$, although *A. crenatiflora* is tetraploid and *A. cristata* includes diploids, tetraploids, and hexaploids, and 3) that *A. thurberi* and *Periptera* form a lineage based on $n = 13$, which probably was derived from *Anoda* sect. *Liberanoda* or its progenitors.

Key words: Malveaceae, *Anoda, Periptera,* chromosomes, hybrids, evolution.

INTRODUCTION

Anoda Cav., which includes 23 species primarily of Mexico (Fryxell 1987), and *Periptera* DC., which is composed of four Mexican species (Fryxell 1974, 1984, 1987), are distinguished from each other primarily by characters that reflect modes of pollination. The flowers of *Periptera* have a red or orange-red, tubular corolla and markedly exserted staminal column. They are assumed to be hummingbird pollinated. The flowers of *Anoda* are white, yellow, lavender, or purple. The corolla tends to be rotate, and the petals exceed or at most are equalled by the staminal column. Pollination is insect mediated.

Cytological and hybridization studies were initiated in *Anoda* and *Periptera* with the expectation they would lead to a better understanding of the nature of the relationship between the two genera, perhaps would suggest relationships to other genera of Malveae, and would provide a framework for considering evolution in *Anoda.* Similar approaches elsewhere in the Malvaceae have proven useful in defining and grouping genera (Bates 1968; Bates and Blanchard 1970, for further discussion), and in giving insights concerning relationships and the course of evolution in a number of taxa, most notably *Gossypium* L. (Saunders 1961; Fryxell 1979) and *Hibiscus* sect. *Furcaria* DC. (Menzel and Wilson 1973).

METHODS

Chromosome counts were made from meioses in pollen mother cells of flower buds collected from plants growing in the wild or grown from seed at Ithaca, New York. Procedures followed those described by Bates and Blanchard (1970). Pollen fertility was measured by scoring percentages of pollen staining with cotton blue in lactophenol. Voucher specimens are deposited in the L. H. Bailey Hortorium (BH). The systematic treatments and nomenclature follow those of Fryxell (1974, 1987).

Jackson (1982, 1984) questioned characterizations of chromosomal pairing

during meiosis and assumptions concerning autoploidy and alloploidy that are widespread in the taxonomic literature. While the relevance of Jackson's comments to this study are recognized, the cytological data available for *Anoda* and *Periptera* are those traditionally presented. Interpretations of chromosomal pairing were made at diakinesis and metaphase I. The terms allopolyploid and autopolyploid are used to distinguish different pathways of euploid development, although the equivocal nature of the concepts they represent is recognized.

PREVIOUS CHROMOSOME COUNTS

Other than numbers reported by Bates and Blanchard (1970), which are considered in the following section, chromosome numbers for *Anoda* have been reported by Davie (1935), Skovsted (1935, 1941), Ford (1938), Delay (1947), and Krapovickas (1957). With the exception of a single count of $2n = 30$, reported by Delay (1947) for *A. parviflora* Cav. (=*A. crenatiflora* Ortega), all counts were of *A. cristata* (L.) Schlecht., although some were reported under the names of *A. hastata* Cav. (=*A. cristata*) or *A. wrightii* A. Gray (=*A. lanceolata* Hook. & Arn.). Chromosome numbers of $n = 15$ or 30 or their somatic equivalents were given in all but one instance. The single exception was a somatic count of $2n = 36$ given for *A. wrightii* (Davie 1935). Using plants grown from seed obtained from Davie, Ford (1938) confirmed the number in a meiotic count, reporting 18 bivalents. He pointed out, however, that these plants did not differ morphologically from those of two other accessions of *A. cristata,* each of which had a chromosome number of $n = 15$. The number $n = 18$ remains unexplained, although it might have arisen as a stabilized derivative of hybridization between diploid and tetraploid or hexaploid forms of *A. cristata.*

RESULTS

Chromosome Numbers

Chromosome numbers determined in this study, as well as eight chromosome counts that were reported by Bates and Blanchard (1970), are given in Table 1. The inclusion of these earlier counts corrects nomenclature and summarizes the findings made in these two related studies.

Among the counts are the first reported numbers for *Periptera* and the following species of *Anoda*: *A. abutiloides* A. Gray, *A. leonensis* Fryxell, *A. palmata* Fryxell, *A. pubescens* Schlecht., *A. thurberi* A. Gray, and *A. zuccagnii* (K. Sprengel) Fryxell. *Anoda crenatiflora* also is probably reported for the first time. The earlier report of that species made by Delay (1947) is at variance with the tetraploid counts consistently made for *A. crenatiflora.* Further, the identification of species from the revision of Hochreutiner (1916) must be regarded as questionable. Counts for *A. reticulata* S. Wats. (Bates and Blanchard 1970) are here referred to *A. pedunculosa* Hochr., while those of *A. acerifolia* (Zuccagni) DC. (=*A. zuccagnii*) belong to *A. cristata.*

The chromosome numbers reported by Bates and Blanchard (1970) established the presence of $n = 15$ in taxa other than *A. cristata* and the occurrence of hexaploids, as well as diploids and tetraploids, in that species. This study confirmed the widespread occurrence of $n = 15$ in *Anoda* and revealed a second

Table 1. Chromosome Counts in *Anoda* and *Periptera*.

Taxon	*n*	Locality and collector
Periptera		
P. punicea	13	Jalisco: *Fryxell, Bates & Blanchard 1623*
	13	Michoacán: *Fryxell, Bates & Blanchard 1625*
	13	Michoacán: *Fryxell & Bates 2159*
Anoda sect. *Anoda*		
A. cristata	15*	Michoacán: *Fryxell 561*
	15	Michoacán: *Fryxell, Bates & Blanchard 1647*
	15	Michoacán: *Fryxell & Bates 2162*
	15	Oaxaca: *Bates & Vivaldi 3442*
	15	Puebla: *Fryxell & Bates 923*
	15	Veracruz: *Fryxell & Bates 928*
	30	Jalisco: *Fryxell, Bates & Blanchard 1611*
	30	Jalisco: *Fryxell, Bates & Blanchard 1620A*
	30	Jalisco: *Bates 3158*
	30	San Luis Potosí: *Fryxell 1074*
	30	Veracruz: *Fryxell & Bates 862*
	45*	Chiapas: *Fryxell & Bates 892*
	45	San Luis Potosí: *Fryxell, Bates & Blanchard 1690A*
	45*	Veracruz: *Fryxell & Bates 851*
	45*	Veracruz: *Fryxell & Bates 931*
A. zuccagnii	15	Colima: *Fryxell, Bates & Blanchard 1614*
	15	Sinaloa: *Fryxell, Bates & Blanchard 1541*
Anoda sect. *Sidanoda*		
A. pentaschista	15*	TX, Cameron Co.: *Bates & Blanchard 2841*
	15*	TX, Nueces Co.: *Bates & Blanchard 2829*
	15	Colima: *Fryxell & Bates 1616*
	15	Oaxaca: *Fryxell & Bates 907*
	15	Sinaloa: *Fryxell & Bates 2115*
Anoda sect. *Liberanoda*		
A. abutiloides	15	Jalisco: *Fryxell & Bates 2136*
A. pubescens	15	Hidalgo: *Fryxell, Bates & Blanchard 1675*
A. thurberi	13	Durango: *Fryxell & Bates 2066*
	13	Tamaulipas: *Fryxell, Bates & Blanchard 1694*
	13	Oaxaca: *Bates & Vivaldi 3436*
	14	Guerrero: *Fryxell & Bates 2164*
Anoda sect. *Cleistanoda*		
A. crenatiflora	30	Hidalgo: *Fryxell & Bates 2177*
	30	Hidalgo: *Fryxell & Bates 2180*
	30	Nuevo León: *Fryxell, Bates & Blanchard 1701*
	30	Nuevo León: *Fryxell, Bates & Blanchard 1707*
A. palmata	15	Jalisco: *Fryxell, Bates & Blanchard 1598*
	15	Michoacán: *Fryxell, Bates & Blanchard 1631*
A. pedunculosa	15	Oaxaca: *Fryxell 1152*
	15*	San Luis Potosí: *Fryxell & Bates 951*
	15*	Tamaulipas: *Fryxell & Bates 948*
Anoda sect. *Clausanoda*		
A. leonensis	15	Nuevo León: *Fryxell, Bates & Blanchard 1697*

* Counts reported by Bates and Blanchard (1970). See text for explanation.

euploid species, the tetraploid *A. crenatiflora.* Unanticipated were the chromosome numbers of $n = 13$ in *P. punicea* (Lag.) DC. and $n = 13$ and 14 in *A. thurberi.*

Meiosis in Nonhybrids

Meiosis in diploid *Anoda* and *Periptera* was unexceptional with consistently high bivalent formation and normal segregation through first and second divisions. Unambiguous counts were possible from diakinesis through telophase II and even into early pollen formation. Although not always fully analyzable, pairing in tetraploid and hexaploid plants also seemed normal and showed no evidence of multivalent formations. Pollen fertility, as determined for at least one individual of each species and each ploidy level of *A. cristata,* ranged from 92 to 100 percent.

As is characteristic of many Malveae, premature disjunction of chromosomes in metaphase I may lead to the presence of unassociated univalents. Although these univalents usually segregate normally, in some instances they do not, and their differential inclusion in daughter cells could lead to the addition or loss of chromosomes in progeny. This is a probable explanation for the presence of a univalent in addition to the normal diploid complement in *A. cristata* (*Bates & Vivaldi 3442*) and *A. thurberi* (*Bates & Vivaldi 3436*).

Hybridization in Anoda *and* Periptera

Natural interspecific hybridization within *Anoda* apparently is rare. Other than a putative hybrid between *A. thurberi* and *A. crenatiflora,* described below, none has been found, although *A. cristata* is sometimes sympatric with other species. *Periptera punicea* and *P. macrostelis* Rose are evidently sympatric in western Jalisco (Fryxell 1974), but no hybrids have been reported, nor are they known between *Anoda* and *Periptera.*

In the greenhouse artifical hybrids between diploid and tetraploid *A. cristata* and between *A. thurberi* and *P. punicea* have been made and are summarized in Table 2. Attempted hybridizations between *A. cristata,* at diploid and tetraploid levels, and *A. crenatiflora* and *A. palmata* produced no viable seed.

Self-compatibility in *Anoda* and *Periptera* also affects hybridization potential. Greenhouse-grown plants of *A. crenatiflora, A. cristata, A. palmata,* and *A. thurberi,* and those of *P. punicea* consistently set fruit following self-pollinations. *Anoda thurberi* proved to be obligately self-pollinated due to the fact that the stigmas did not extend beyond the dehiscing anthers. Small-flowered forms of *A. crenatiflora* were functionally cleistogamous with pollination taking place before the corolla opened.

Meiosis in Hybrids

Among the archaeological ruins on Monte Albán *A. crenatiflora* (*Bates & Vivaldi 3437*), *A. thurberi* (*Bates & Vivaldi 3436*), and *A. cristata* (*Bates & Vivaldi 3439*) occur sympatrically. In one intermingled population a putative hybrid (*Bates & Vivaldi 3438*) between *A. thurberi* ($n = 13$) and *A. crenatiflora* ($n = 30$) was found. Meiosis in this plant exhibited little pairing. In most cells only one or two bivalents were formed, although in one instance six bivalents were observed. The remaining chromosomes appeared as univalents. Pollen formation was low and anther dehiscence rare.

Table 2. Hybrids in *Anoda* and *Periptera*.

Collection number	♀ Parent, *n*, collection number	♂ Parent, *n*, collection number	Maximum pairing
*B & V 3438**	*A. crenatiflora*, 30 (*B & V 3437*)	*A. thurberi*, 13 (*B & V 3436*)	6 II, ca. 30 I
72-376	*A. cristata*, 15 (*F 561*)	*A. cristata*, 15 (*FBB 1647*)	15 II
72-377	*A. cristata*, 15 (*F 561*)	*A. cristata*, 30 (*FBB 1611*)	10 II, 1 III, ca. 22 I
72-379	*A. cristata*, 15 (*FBB 1647*)	*A. cristata*, 30 (*FBB 1611*)	15 II, 15 I
73-162	*A. thurberi*, 13 (*FBB 1694*)	*P. punicea*, 13 (*FBB 1625*)	13 II
73-163	*A. thurberi*, 14 (*FB 2164*)	*P. punicea*, 13 (*FBB 1625*)	13 II
73-164	*A. thurberi*, 13 (*FB 2066*)	*P. punicea*, 13 (*FBB 1625*)	13 II

* Parentage assumed, male and female contributors not known.

In *A. cristata* meiotic analyses of two hybrids resulting from crosses between diploid plants (*Fryxell 561 & Fryxell, Bates & Blanchard 1647*) and tetraploid plants (*Fryxell, Bates & Blanchard 1611*), showed rather different chromosome pairing. In one hybrid (72-379) up to 15 bivalents were formed, although as few as 12 were found in some cells. The remaining chromosomes were unassociated. In the other hybrid (72-377) maximum pairing was less, with as many as ten pairs found in only one cell. Although stainability was high, pollen of both hybrids varied markedly in size, presumably a reflection of their different chromosome numbers.

Chromosome pairing in F_1 hybrids between *P. punicea* and *A. thurberi* tended to be complete. Generally 13 bivalents were formed. Univalents, if present, were no more than four and seemed attributable to early disjunction. An expected extra chromosome in plants (73-163) derived from the cross involving *A. thurberi* with $n = 14$ (*Fryxell & Bates 2164*) did not appear, although an extra chromosome was present in one F_1 (73-162) in which *Fryxell, Bates & Blanchard 1694* was the *A. thurberi* parent. Despite pairing that is in accord with that observed in nonhybrid species, pollen fertility in two F_1's was measured at 65 and 68 percent. In a sample of five F_2's, derived from selfed F_1's, pollen fertility ranged from 87 to 98 percent.

DISCUSSION AND CONCLUSIONS

The discussion is organized around three themes: 1) the relationships of *Anoda* to other genera of Malveae, 2) evolution in *Anoda*, and 3) the relationship between *Anoda* and *Periptera*.

Relationships of Anoda

The morphology of *Anoda* places it among the abutiloid genera of the tribe Malveae, but none of these genera show particular morphological affinities to it

(Fryxell 1987), and only *Bakeridesia* Hochr. (Bates 1973) and *Bastardiastrum* (Rose) Bates (Bates 1978) share with it a gametic number of $n = 15$.

In his systematic treatment Fryxell (1987) placed the 23 species of *Anoda* in six sections. Chromosome numbers are now known for ten species, distributed through five of the six sections. The occurrence of species with a chromosome number of $n = 15$ in each of the five sections argues that this number is basic in the genus. Since base chromosome numbers of abutiloid genera are $\bar{x} = 6$, 7, and 8, $n = 15$ in *Anoda* apparently was derived secondarily. One possibility would be direct formation as an allotetraploid combining base numbers of seven and eight. Other possibilities are found in derivation from a stabilized polyploid ancestor with a gametic number of $n = 14$, 15, or 16. The origin and relationships of *Anoda* cannot be determined more precisely from existing data.

Evolution in Anoda

Speciation in *Anoda* has occurred primarily at the diploid level. Direct evidence concerning interspecific genetic isolation among the $n = 15$ diploids is limited, but does reveal genic/chromosomal barriers between *A. cristata* and both *A. palmata* and *A. crenatiflora* and between *A. thurberi* and *A. crenatiflora.* Similar barriers may exist between other species or species groups of the genus.

The tetraploid *A. crenatiflora* ranges through Mexico to Texas and Arizona in the north. As a member of the relatively homogeneous section *Cleistanoda* A. Gray, either allo- or autoploid origin is possible. However, if the species is an allopolyploid, the identity of its diploid progenitors, if extant, is not obvious.

Anoda cristata is the most widely distributed and morphologically variable species of the genus. In view of the sample size, statements concerning morphological differentiation among the three ploidy levels are premature, although there are suggestions of certain trends. For example, diploids have mericarps in which the endocarp is absent, is present as a partial, dorsally reticulate hood, or encloses the seed in a reticulate covering. In tetraploids the endocarp is absent or present as partial hood; while in hexaploids the endocarp appears only as a partial hood. Further, there appears to be altitudinal distribution of ploidy levels. Tetraploids were collected from near sea level to about 460 meters, hexaploids between 675 and 1230 meters, and diploids between 1385 and 1850 meters.

When viewed broadly, however, the similar patterns of morphological variation found at each ploidy level in *A. cristata* and the closely related diploid *A. zuccagnii* suggest the complex is autoploid, as has been proposed for other Malveae. For example, Bates, Dorr and Blanchard (in press) have speculated autoploid origins for tetraploid *Callirhoe involucrata* (T. & G.) A. Gray and hexaploid *C. papaver* (Cav.) A. Gray. Arguing against autoploidy in *A. cristata* is the strong preferential pairing observed at all ploidy levels and in one of the diploid/tetraploid hybrids, the other being more equivocal. De Wet and Harlan (1972), however, have pointed out the rapidity with which autoploids can establish normal pairing, and Jackson (1982) raises questions concerning traditional interpretations of polyploidy based on the kinds of pairing data available in this study. Whatever the extent of genomic differentiation in *A. cristata,* it is probably genic in character and represents little structural chromosomal differentiation.

Relationships between Anoda, A. thurberi, *and* Periptera

Chromosome numbers of $n = 13$ and 14 observed in *A. thurberi* and $n = 13$ in *P. punicea* were unexpected for two reasons. First, in the Malveae aneuploid differences among species of the same genus are relatively uncommon. Second, except for the floral morphology of *P. punicea,* the two species are accommodated in *Anoda.*

In the Malveae apparent aneuploid reduction from $\bar{x} = 8$ to 7, 6, and 5 has been of major importance in generic evolution (Bates and Blanchard 1970). At these chromosome levels dibasic chromosome numbers within a genus are uncommon. They are restricted to the strongly circumscribed *Herissantia* Medic. ($n = 6$ and 7) and the large morphologically variable genera *Abutilon* Mill. and *Sida* L., in which either $\bar{x} = 7$ or 8 characterize sectionally differentiated lineages. As *Sida* and *Abutilon* undergo revision, the tendency has been to recognize some lineages generically, as illustrated by the *Sida* segregates of Fryxell (1978). Elsewhere in the Malveae, dibasic numbers are occasional in genera at higher ploidy levels, e.g., *Callirhoe* Nutt. ($\bar{x} = 14$, 15) (Bates, Dorr and Blanchard in press). *Periptera* is exceptional in the Malveae in that it differs from its closest relative, *Anoda,* in having two fewer gametic chromosomes. The situation in *A. thurberi* is more equivocal with apparent loss of a single chromosome in one population, two in the others.

The means by which chromosome numbers have been reduced in *P. punicea, A. thurberi,* and in other Malveae are not known. The presence of unpaired univalents during meiosis and failure to incorporate them into daughter cells suggests a mechanism for chromosome reduction, although such reductions could result in genic deletions. There is no evidence of translocation induced reductions.

Anoda thurberi, ranging from Arizona through Mexico to Oaxaca, belongs to the section *Liberanoda* Fryxell, which is notable in having mericarps without an endocarp—presumably a derived condition in the genus. Within the section, *A. thurberi* is distinguished in having somewhat clavate stigmas and bluish-lavender corollas that barely exceed the calyx. Fryxell (1987) notes that it shows no clear affinities with the other species of the section. Two of these, *A. abutiloides* and *A. pubescens,* have a gametic number of $n = 15$. The others are unknown chromosomally.

Direct evidence of a chromosomal relation between *A. thurberi* and other species of *Anoda* is available only from the putative hybrid between *A. thurberi* and tetraploid *A. crenatiflora.* In view of the differences in ploidy levels and sectional affiliations of the parents, the significance of the hybrid is largely found in its vigorous growth and flower production, rather than limited bivalent formation.

In addition to differences in corolla and staminal column characters, *Periptera* is distinguished from *Anoda* by having clavate rather than abruptly capitate stigmas. If these floral traits were discounted, then species of *Periptera* probably would be placed in *Anoda* sect. *Liberanoda,* although their carpel number (10–12) extends that characteristic of the section (6–10). Among the species of section *Liberanoda, A. pubescens, A. speciosa* Fryxell, and *A. henricksonii* M. C. Johnst., as well as *A. thurberi,* have flowers with the staminal column subequal to the campanulate corollas, a condition probably ancestral to the exserted staminal

column of *Periptera.* F_1 hybrids between *P. punicea* and *A. thurberi* essentially duplicate the subequal corolla and staminal column, and F_2's segregate for a wide variety of floral types.

In an evolutionary context the derivation of *A. thurberi* and *Periptera* from section *Liberanoda* or its progenitors could have occurred as a single event or as independent events. The high level of chromosome pairing and relatively high levels of pollen fertility in hybrids between *A. thurberi* and *P. punicea* argue against independent events. As a single lineage, chromosomal reduction to $n = 13$ either has been accomplished stepwise, initially to $n = 14$, then to $n = 13$, or with more drastic chromosomal reorganization in a single step. In the latter case those plants of *A. thurberi* with $n = 14$ would be derived secondarily and perhaps only as sporadic variants, since the extra chromosome was not carried into hybrids between that form and *P. punicea.*

Morphology tends to favor reduction to $n = 13$ in a single step. If $n = 14$ were to represent the intermediate step at which *A. thurberi* was differentiated, then subsequent derivation of $n = 13$ *A. thurberi* without morphological change, followed by diversification of *Periptera,* is implied. When one considers the reduced floral parts and autogamous breeding systems of *A. thurberi,* this seems less probable than derivation of the lineage from an ancestor with a generalized floral form, followed by floral divergence, as it is now represented in *A. thurberi* and *Periptera.* The petal and staminal column characteristics of *A. pubescens* are perhaps representative of those hypothesized to be ancestral. The fact that Fryxell (1974) described collections of *A. pubescens* as *P. grandiflora* Fryxell strengthens that contention.

Regardless of sequence and details of change, acceptance of *A. thurberi* and *P. punicea* as members of a single lineage and more closely related to each other than to the other species of *Anoda* has taxonomic implications. Either *Periptera* should be returned to *Anoda,* its species placed either in the section *Liberanoda* or with *A. thurberi* in a new section, or *A. thurberi* should be transferred to *Periptera.* Morphology favors the first alternative; chromosomal discontinuity and presumed genetic isolation the second.

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